

einer durchschnittlichen Reisegeschwindigkeit von etwa 50 km/h (KOCK und SCHWARTING 1987) würden die Tiere „termingerecht“ in den osteuropäischen Sommergebieten ankommen.

Die Rauhhaufledermäuse sind wahrscheinlich Saisonwanderer, die das Gebiet der Bundesrepublik überfliegen oder an wenigen besonders begünstigten Stellen überwintern. Die Art *Pipistrellus nathusii* fällt demnach auch unter die Bonner Konvention vom 23. Juni 1979 über das Übereinkommen zur Erhaltung wandernder wildlebender Tierarten (ERZ 1981). In die rote Liste der gefährdeten Tiere und Pflanzen ist sie unter die Kategorie II (Gefährdete Durchzügler, Überwinterer, Übersommerer, Gäste usw.) einzuordnen (BLAB et al. 1984).

Danksagung

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Zusammenfassung

Anhand von Literaturdaten wird das Vorkommen der Rauhhaufledermaus in Baden-Württemberg beschrieben. Es wurden insgesamt 508 Funde ausgewertet. Dabei ergaben sich Fundhäufungen im Herbst und im Winter (Abb. 2). Während das Hauptmaximum im September mit einer Herbstwanderung in Verbindung gebracht werden kann, ist das Nebenmaximum im Januar eher auf Meldungen von Winterverlusten zurückzuführen. Es wird ein Zugweg von Sommerquartieren in der DDR oder Polen durch das Neckartal zum Bodensee und von dort aus weiter durch das Schweizer Mittelland oder die Burgundische Pforte in die Winterquartiere erwogen (Abb. 5). Offen bleibt die Frage, wann und auf welchem Weg die Tiere in die Sommerquartiere zurückkehren.

Literatur

- AELLEN, V. (1961): La Baguement des Chauves-souris au Col de Bretolet (Valais). Arch. Sci. 14, 365–392.
- BAUER, K.; WIRTH, J. (1979): Die Rauhhaufledermaus (*Pipistrellus nathusii* Keyserling und Blasius, 1839) (Chiroptera, Vespertilionidae) in Österreich. Ann. Naturhistor. Mus. Wien 82, 373–385.
- BLAB, J.; NOWAK, E.; SUKOPP, H. (1984): Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland. Greven: Kilda.
- CLAUDE, C. (1976): Funde von Rauhhaufledermäusen, *Pipistrellus nathusii* in Zürich und Umgebung. Myotis 14, 30–36.
- DIETERICH, J. (1982): Vergleichende Beobachtungen über den Fledermausbesatz in verschiedenen Nistgeräten nach Untersuchungen in Schleswig-Holstein. Myotis 20, 38–44.
- ERZ, W. (Hg.) (1981): Schutz wandernder Tierarten. Greven: Kilda.
- FELTEN, H.; KLEMMER, K. (1960): Fledermäuse des Rhein-Main-Lahn-Gebietes. Bonn. zool. Beitr. Sonderheft 11, 166–188.
- GEBHARD, J. (1983): Die Fledermäuse in der Region Basel (Mammalia: Chiroptera). Verhandl. Naturf. Ges. Basel. 94, 1–42.
- HAENSEL, J. (1967): Notizen über 1963–1966 insbesondere in Berlin aufgefundene Fledermäuse. Milu 2, 313–322.
- HANAK, V.; GAISLER, J. (1976): *Pipistrellus nathusii* (Keyserling et Blasius, 1839) (Chiroptera: Vespertilionidae) in Czechoslovakia. Vest. Cs. spol. zool. 40, 7–23.
- HEISE, G. (1982): Zu Vorkommen, Biologie und Ökologie der Rauhhaufledermaus (*Pipistrellus nathusii*) in der Umgebung von Prenzlau (Uckermark), Bezirk Neubrandenburg. Nyctalus NF1, 281–300.
- HIEBSCH, H. (1983): Faunistische Kartierung der Fledermäuse in der DDR. Teil 1. Nyctalus NF1, 489–503.
- ISSEL, B.; ISSEL, W.; MASTALLER, M. (1977): Zur Verbreitung und Lebensweise der Fledermäuse in Bayern. Myotis 15, 19–97.
- KLAWITTER, J. (1974): Zum Vorkommen von *Pipistrellus nathusii* in Westberlin. Myotis 12, 44–45.
- KOCK, D. (1981): Rauhhaufledermäuse im Rhein-Main-Gebiet. Natur und Museum 111, 10–24.
- KOCK, D.; SCHWARTING, H. (1987): Eine Rauhhaufledermaus aus Schweden in einer Population des Rhein-Main-Gebietes. Natur und Museum 117, 20–29.
- KULZER, E. (1986): Winterschlaf von Abendseglern (*Nyctalus noctula*) in künstlichen Quartieren – ein Beitrag zum Fledermausschutz. Protokoll der 7. Tagung der AG-Fledermausschutz, Tübingen.

- KULZER, E.; BASTIAN, H. V.; FIEDLER, M. (1987): Die Fledermäuse in Baden-Württemberg. Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ., 50.
- MÜLLER, A.; WIDMER, M. (1983): Bestand und Verbreitung der Fledermäuse des Kantons Schaffhausen und Umgebung. Abschlußbericht, 1–82.
- ROER, H. (1971): Weitere Ergebnisse und Aufgaben der Fledermauserhebung in Europa. Decheniana Beih. 18, 121–144.
- (1974): Die Raubhautfledermaus (*Pipistrellus nathusii*) in Mitteleuropa. Myotis 11, 18–27.
- (1976): Weitere Nachweise der Raubhautfledermaus (*Pipistrellus nathusii*). Myotis 13, 65–67.
- SCHMIDT, A. (1977): Ergebnisse mehrjähriger Kontrollen von Fledermäusen im Bezirk Frankfurt (Oder). Naturschutzarb. in Berlin u. Brandenburg 13, 42–51.
- (1978): Zum Geschlechtsdimorphismus der Raubhautfledermaus (*Pipistrellus nathusii*) nach Funden im Bezirk Frankfurt/O. Nyctalus NF1, 41–46.
- SCHÖBER, W. (1960): Zur Kenntnis mitteleuropäischer Fledermäuse. Bonn. zool. Beitr. Beih. 18, 105–111.
- STRELKOV, P. P. (1969): Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. Ac. Zool. Cracov. 14, 393–439.
- STUTZ, H. P.; HAFFNER, M. (1985): Geschlechtsspezifische saisonale Anwesenheit einiger mitteleuropäischer Fledermausarten in der Zentral- und Ostschweiz. Mitt. Naturf. Ges. 32, 1–5.
- VIERHAUS, H.; BÜLOW, B. VON (1978): Zwei neue Nachweise der Raubhautfledermaus *Pipistrellus nathusii* (Keyserling und Blasius, 1839) aus Westfalen. Natur und Heimat 38, 65–70.
- WIJNGAARDEN, A. VAN; LAAR, V. VAN; TROMMEL, M. D. M. (1971): De verspreiding van de uederlandse zoogdieren (Mammalia: Insectivora, Chiroptera, Rodentia, Lagomorpha, Carnivora, Pinnipedia, Artiodactyla. Lutra 13, 2–41.

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The anatomy of the stomach and caecum of the Samango monkey, *Cercopithecus mitis erythrarchus* Peters, 1852

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Abstract

An investigation of the gastric and caecal anatomy of *Cercopithecus mitis erythrarchus* revealed a simple glandular stomach and a sacculated caecum. The unilocular glandular stomach is typical of cercopithecine primates. The caecum and colon possess well-developed taeniae and haustra, and provide microhabitats for numerous symbiotic bacteria. The morphological observations are interpreted in terms of the functional digestive process of this primarily frugivorous primate.

Introduction

Herbivorous mammals can be classified into two broad categories according to their digestive strategy and gut adaptations that accommodate microbial fermentation (PARRA 1978): firstly, those animals with an enlarged foregut that is the main site of microbial activity and in which microbial fermentation precedes gastric intestinal digestion, or secondly, those animals with an enlarged hindgut, in which gastric intestinal digestion of the diet occurs before microbial fermentation (PARRA 1978). Many fermentative bacteria are cellulolytic, and for those animals with a diet rich in structural carbohydrates a large fermentation chamber in the digestive tract is necessary.

Old World monkeys of the subfamily Colobinae are predominantly folivorous (CHIVERS and HLADIK 1980), and differ from all other primates in the large size and anatomical complexity of the stomach (BAUCHOP and MARTUCCI 1968). Consequently, considerable literature has accumulated on the ruminant-like, microbial gastric digestion occurring in the stomach (BAUCHOP and MARTUCCI 1968; OHWAKI et al. 1974; BAUCHOP 1978) and on the microbiology of the colobine stomach (BAUCHOP 1971).

The more typical Old World monkeys of the subfamily Cercopithecinae are predominantly frugivorous-omnivorous, and the stomach is a simple, smooth-walled sac (HILL 1958). Recent investigations on volatile fatty acid (VFA) concentrations (the breakdown products of microbial fermentation) and digesta movement in the gastrointestinal tracts of a number of Cercopithecinae (CLEMENS and PHILLIPS 1980; CLEMENS and MALOY 1981) have demonstrated that the stomach contains an acidic environment unsuitable for prolonged microbial activity. From the high concentrations of VFAs recorded in the large intestine of these primates, it appears that the caecum and colon are important sites of microbial activity and VFA production.

An extensive study on the socioecology and feeding ecology of the Samango monkey *Cercopithecus mitis erythrarchus* is currently in progress in Natal (LAWES pers. comm.). To examine the Samango in relation to the two digestive strategies and to relate the diet to current concepts of digestion theory, a detailed knowledge of the monkey's gastric morphology was required. A preliminary examination of the stomach and caecum of the Samango monkey was therefore initiated to determine the gross anatomy, histology and ultrastructure of the respective organs, and to correlate anatomy with diet and function.

Materials and methods

One weaned juvenile female and one adult female Samango monkey were used for this examination. The shot animals were dissected in the field immediately after death and photographed to display the position of the organs in situ. The pH in the proximal and distal stomach regions, mid-region of the small intestine, caecum, and ascending and descending colon was measured using a single glass probe electrode (Model TC pH 800) placed in a small incision in the GIT wall.

Small sections of stomach and caecal tissue (5 mm × 5 mm) were fixed in 3 % buffered glutaraldehyde for scanning and transmission electron microscopy. Thereafter whole organs were placed in Bouin's fixative for 18 h. After fixation the organs were bisected and preserved in 70 % alcohol. One half of each organ was used for gross morphological analysis, the other for histological examination using standard tissue preparation techniques (HUMASON 1962). Haematoxylin and eosin were used as general tissue stains, while Alcian blue was used to confirm mucus (polysaccharide) secretion (HUMASON 1962).

For electron microscopy tissue was removed from the gut and postfixed in 1 % osmium tetroxide in 0.05 M sodium-cacodylate buffer, then dehydrated in a graded alcohol series. Material for transmission electron microscopy (TEM) was further dehydrated in propylene oxide and embedded in Epon. Sections were cut on an LKB Ultratome 3 ultramicrotome, stained with uranyl acetate and lead citrate and viewed with a Hitachi Model HU-11E-1 transmission electron microscope. For scanning electron microscopy (SEM), material was critical-point dried, coated with gold palladium and viewed with a Hitachi S-570 scanning electron microscope.

Results

pH

pH readings recorded at different sites along the GIT are given in the Table.

Table. pH readings along the GIT of adult and juvenile Samango monkeys

	Stomach		Section of tract	Caecum	Ascending colon	Descending colon
	Fundus	Antrum	Mid small intestine			
Adult	5.00	3.13	6.31	5.97	6.25	6.47
Juvenile	5.19	3.08	6.53	5.58	6.69	6.90

Topography in situ

The stomach of *C. m. erythrarchus* extends laterally across the abdominal cavity and occupies approximately one quarter by volume of the cavity. The small intestine, caecum, colon and rectum fill the remainder of the cavity (Fig. 1). The caecum is located in the lower right region of the abdominal cavity, lying directly against the abdominal wall (Fig. 1) and partially obscured in the distal region by the mesentery of the small intestine. The large, haustrated transverse colon is prominent, possessing distinct taeniae (Fig. 1) along its entire length.

Gross morphology

Stomach

The stomach is a simple unilocular glandular sac (Fig. 2a), with the oesophagus entering the mid-dorsal region of the corpus (forestomach). Sinistral to the gastro-oesophageal junction the fundus extends laterally, forming a slightly globular pouch. Dextral to the junction, the lesser curvature immediately reflects to form the pars pylorica (Fig. 2a); the antrum (hindstomach) extends from the oesophageal opening, and curves dorsally forming

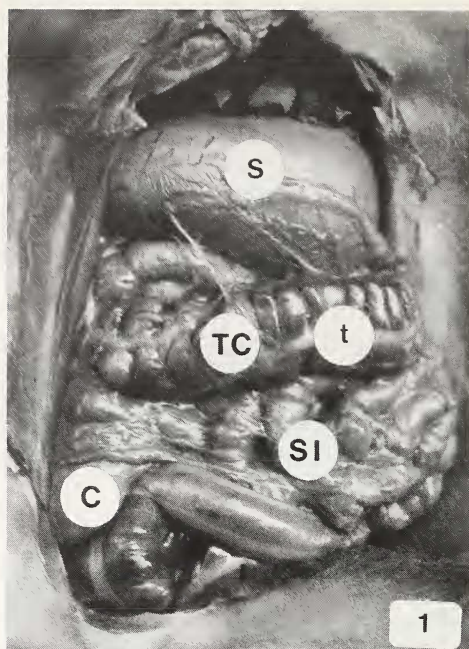


Fig. 1. The disposition of the GIT within the abdomen of *C. m. erythrarchus*. Note the haustrated transverse colon (TC) and the taenia (t). SI = small intestine, C = caecum, S = stomach

the pars pylorica. The only apparent difference between the stomachs of juvenile and adult monkeys was the increased folding of the stomach wall in the adult.

Caecum

The caecum of adult *C. m. erythrarchus* displays several haustum-like sacculations and two prominent, laterally situated taeniae which extend along the length of the colon. The ileum enters the caecum at the border between the ampulla caeci and corpus caeci (Fig. 3). Distal to this opening at the end of the ampulla is the caecocolic junction, from which the proximal colon emerges (Fig. 3).

Although the general form of the adult and juvenile caeca is similar, they differ markedly in the extent of haustration and folding of the internal mucosal surface. In the adult (Fig. 3), a deep sacculation separates the corpus caeci and ampulla; it is likely that digesta is directed into the corpus caeci via a muscular valve at the ileocaecal junction (Fig. 3). The extent of the internal folding is similar in the caecum and proximal colon. The caecum of juveniles (Fig. 4), in comparison, is a large unilocular sac with no distinct separation between the corpus caeci and ampulla caeci.

Histology

Stomach

A typically mammalian gastric tissue plan (WEISS and GREEP 1977; HAM and CORMACK 1979) is present (Fig. 5). The muscularis externa is generally thicker in the corpus than in the antrum, where the circular muscle layer (stratum circulare) is approximately three times thicker than the longitudinal layer (stratum longitudinale).

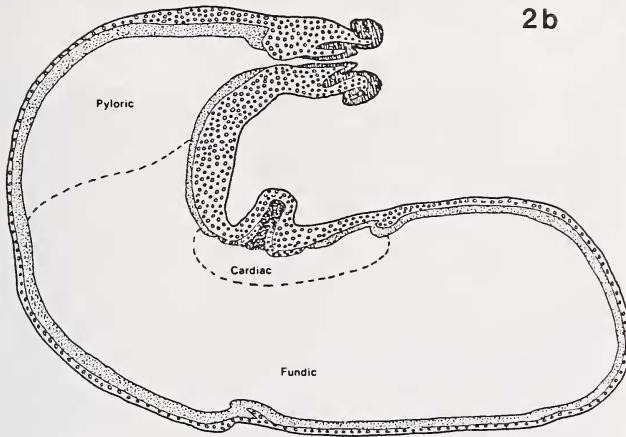
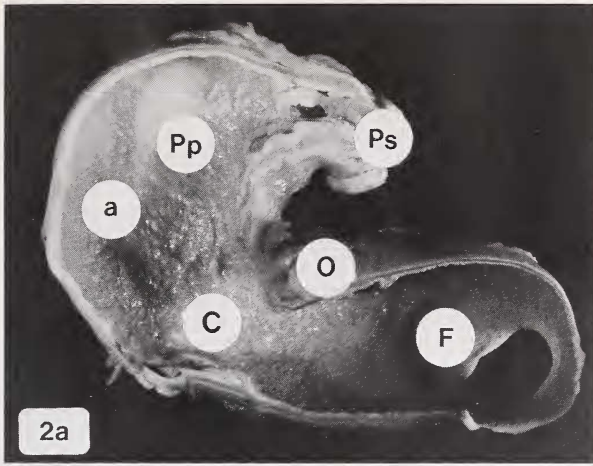


Fig. 2a. A photograph of a bisected stomach of *C. m. erythraeus* (juvenile). F = fundus, C = corpus, Pp = pars pylorica, O = oesophagus, Ps = pyloric sphincter, a = antrum. - b: Semi-diagrammatic drawing of a bisected stomach showing the regions of glandular tissue

A submucosa of loose connective tissue is of constant thickness in the corpus and antrum (Fig. 5). The muscularis mucosa is continuous with that of the oesophagus, and lamina propria extends between the glandular tissue.

The mucosal lining of the stomach is histologically divisible into cardiac, fundic and pyloric regions. The cardiac tissue in the stomach extends 1-1.5 cm radially from the cardiac orifice (Fig. 2b). The short, branched cardiac glands possess wide foveolae with closely packed mucous neck cells (Fig. 6). These cells continue for some distance into the tubules of the glands. Parietal (oxyntic) and chief (or peptic or zymogen) cells are present

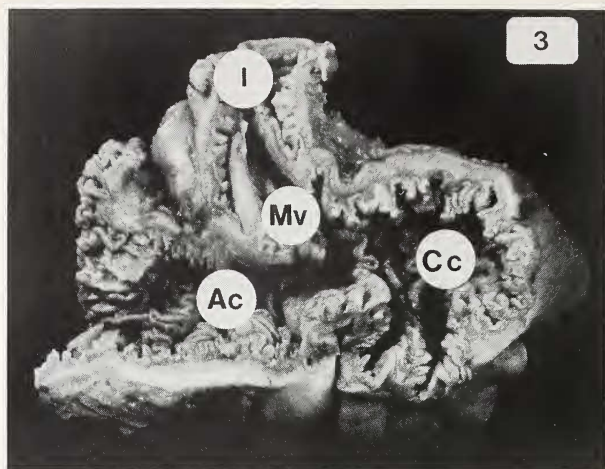


Fig. 3. A photograph of the bisected caecum of an adult *C. m. erythrarchus*, showing the deep haustration between corpus caeci (Cc) and ampulla caeci (Ac), and the muscular valve (Mv) at the ileocaecal junction. I = ileum

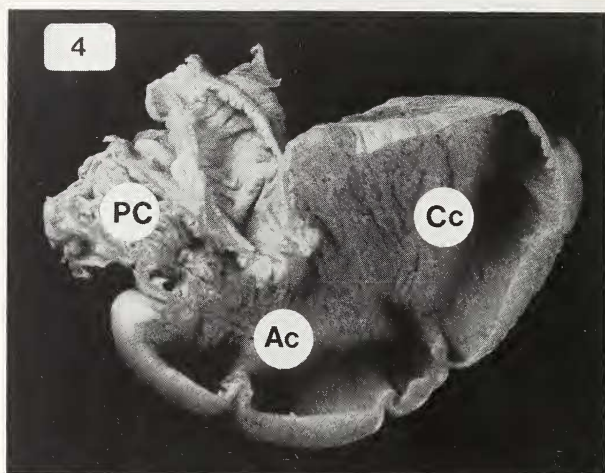


Fig. 4. A photograph of the bisected caecum of a juvenile *C. m. erythrarchus*. Cc = corpus caeci, Ac = ampulla caeci, PC = proximal colon

(Fig. 6), but their relative scarcity and the large numbers of closely packed mucous cells is characteristic of cardiac glands.

In the fundic region the glands are long and tubular with narrow foveolae and extend through the mucosa to the muscularis mucosa (Fig. 7). A histological stratification typical for mammalian fundic glands is evident, i.e., cuboidal neck cells, followed by mid-region mucous neck cells, and chief cells at the base, with parietal cells scattered throughout the gland, but predominantly in the mid-gland regions (Fig. 7).

In the pyloric region parietal and chief cells are absent. Typically only one cell type is evident, a mucus-secreting cell similar to the mucous neck cells of the fundic region (Fig. 8). Pyloric glands are highly coiled and possess wide foveolae (Fig. 8).

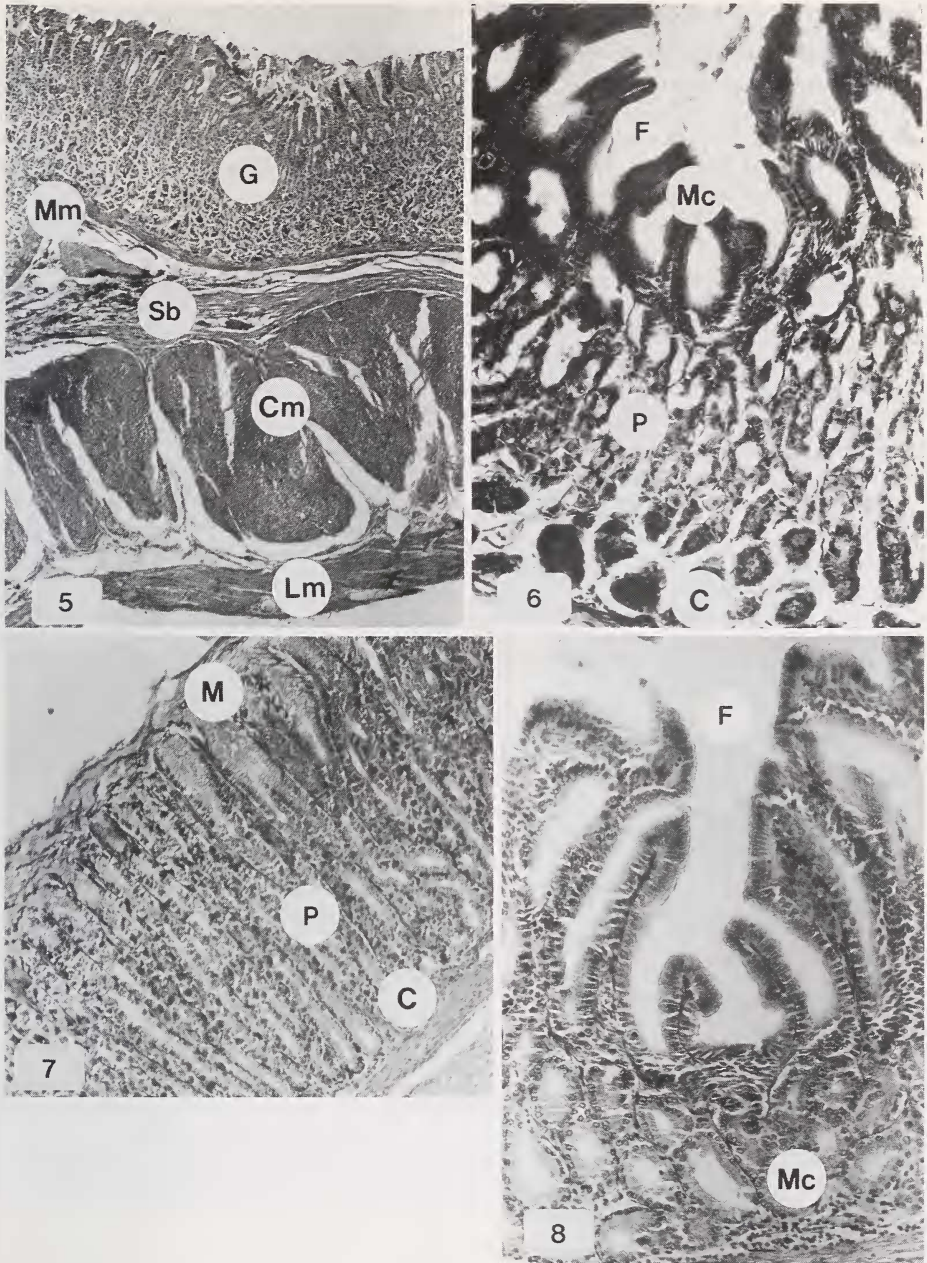


Fig. 5. A typical mammalian gastric tissue plan was observed. G = glandular tissue, Mm = muscularis mucosa, Sb = submucosa, Cm = circular muscle layer, Lm = longitudinal muscle layer. - Fig. 6. A section of the cardiac glands showing mucoid neck cells (Mc), parietal cells (P) and chief cells (C). F = foveolus of gland. - Fig. 7. A photograph of a section of fundic glands showing the long, tubular nature of the glands. M = mucus, P = region of parietal cells, C = region of chief cells. - Fig. 8. A photograph of a pyloric gland. F = foveolus of gland, Mc = mucus-secreting cells

Caecum

The caecum also possesses a typical mammalian alimentary tissue plan (Fig. 9). The muscularis externa is continuous with that of the ileum and the proximal colon; the submucosa of loose connective tissue maintains a constant thickness throughout the caecum (Fig. 9). The muscularis mucosae is continuous with that of the ileum and colon. A lamina propria of fine connective tissue and elastin fibres is present above the muscularis mucosae and extends between the glandular tissue (Fig. 9).

The surface epithelium consists of predominantly columnar absorptive cells, and numerous crypts with wide openings that extend along the length of the caecum. These glands contain numerous columnar mucous goblet cells (Fig. 10).

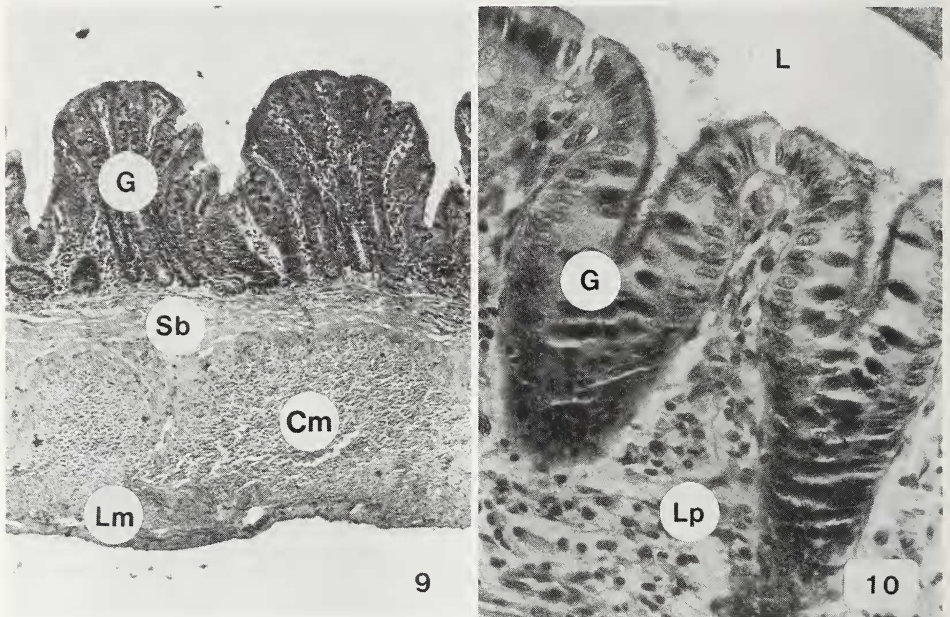


Fig. 9. A photograph showing the typical mammalian alimentary tissue plan of the caecum. G = glandular region, Sb = submucosa, Cm = circular muscle layer, Lm = longitudinal muscle layer. — Fig. 10. A photograph of two caecal crypts, showing the abundance of goblet cells (G) and the lamina propria (Lp) between the crypts

Histologically, no differences are apparent between the ampulla and corpus caeci, or between juvenile and adult caeca.

Electron microscopy

Stomach

Material examined by SEM was limited to fundic and pyloric tissue. The pyloric region of the stomach is characterised by deep infoldings (Fig. 11). The pyloric glands open into these recesses and the columnar epithelial cells show a typical “cobblestone” surface appearance (Fig. 11).

Numerous sessile filamentous bacteria in palisade configuration were present in the adult fundus (Fig. 12), while in the juvenile few isolated pockets of shorter bacteria were found (Fig. 13). No bacteria were present in the pars pylorica of either monkey.

Caecum

SEM observations support the light-microscopic findings. The surfaces of both the corpus caeci and ampulla caeci contain numerous crypts and a dense covering of long, threadlike microvilli (Figs. 14 and 15). TEM sections through the caecal crypts show that the crypts are surrounded by tall columnar epithelial and numerous goblet cells (Fig. 16). The nuclei of the goblet cells are basally situated and numerous supranuclear mitochondria are present.

Large numbers of cocco-bacilli and cocci occur, apparently unattached, among the

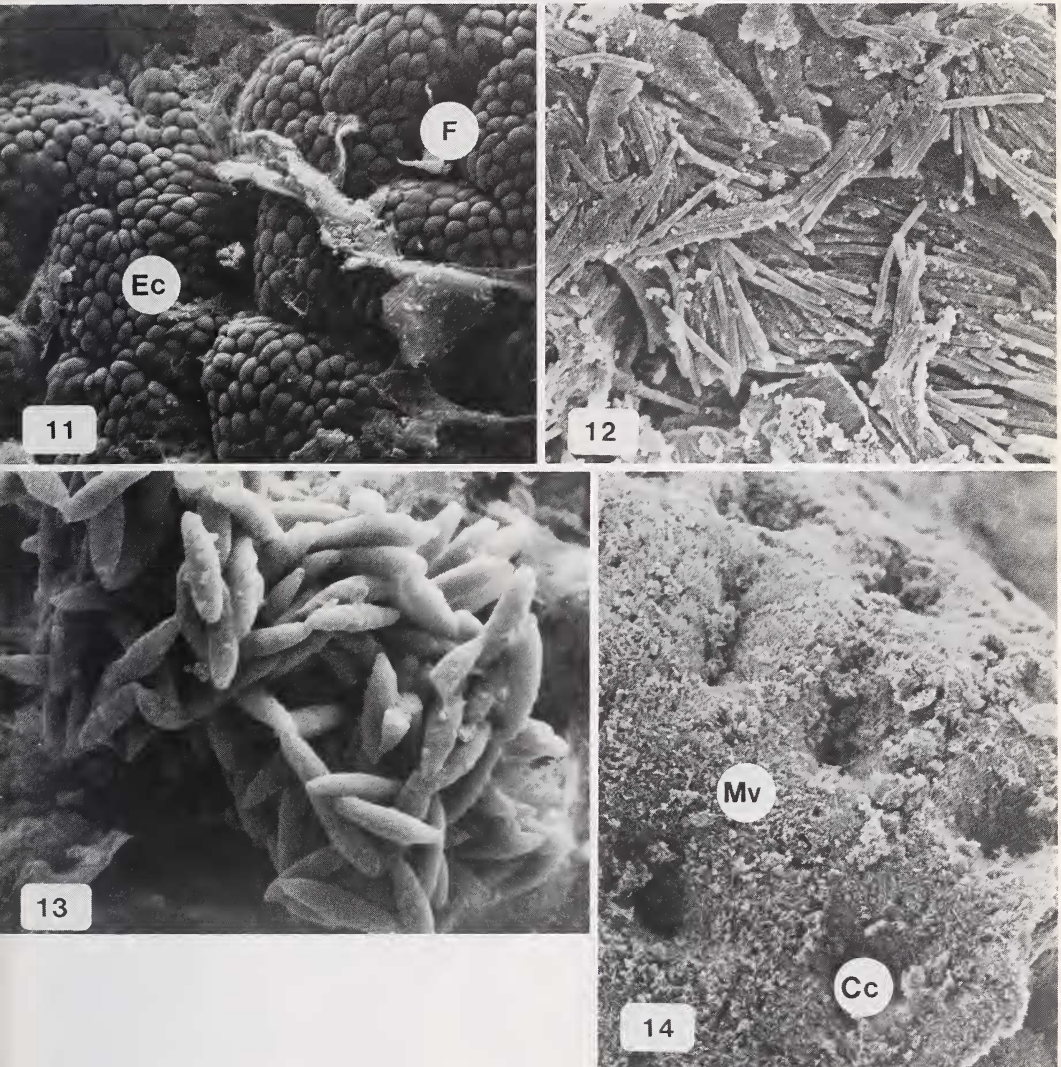


Fig. 11. A scanning electron micrograph of two pyloric glands, showing the foveola of the glands (F) and the typical cobblestone appearance of epithelial cell surfaces (Ec). - Fig. 12. Bacilli in the fundus of adult *C. m. erythrarchus*. - Fig. 13. Cocco-bacilli in the fundus of juvenile *C. m. erythrarchus*. - Fig. 14. A micrograph of the caecal epithelial surface showing the dense layer of microvilli (Mv) and the caecal crypts (Cc)

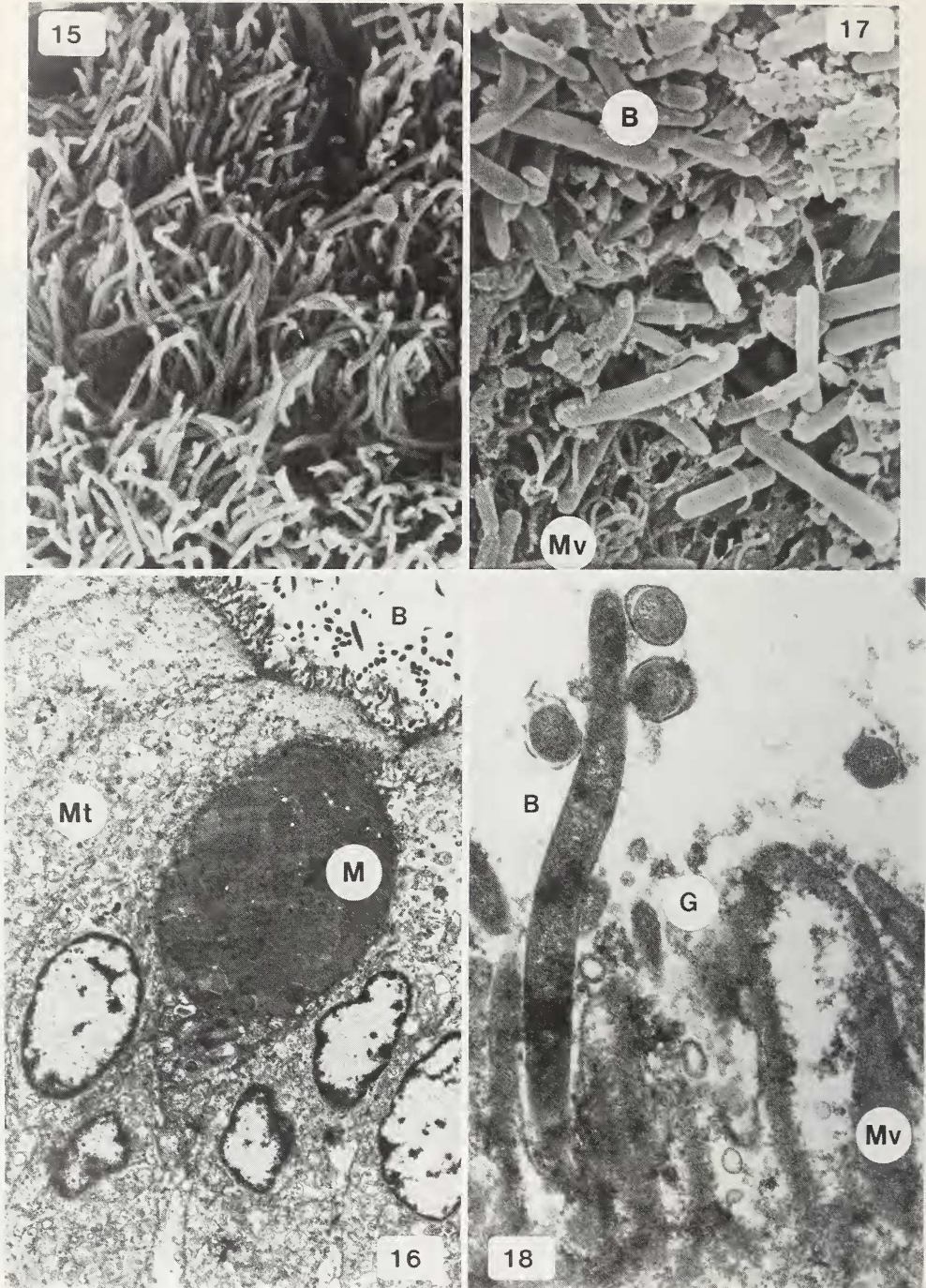


Fig. 15. A high-power micrograph of caecal microvilli. - *Fig. 16.* A transmission electron micrograph of a section through a caecal crypt, showing bacteria (B) in the crypt lumen and the mucoid body (M) of a goblet cell. Mt = mitochondria. - *Fig. 17.* A micrograph showing bacteria (B) on the caecal surface. Mv = microvilli. - *Fig. 18.* A micrograph showing the close association of a bacterium (B) with the microvilli (Mv). G = glycocalyx

mucus and food particles on the caecal surface (Fig. 17) and also penetrate into the caecal crypts. Under TEM the close association of the bacteria in the crypt lumen with the microvillar border is striking (Fig. 18). Many of the bacteria are lodged between the microvilli and appear to indent the apical plasma membrane of the cells (Fig. 19), but no bacterial penetration of cells is evident.



Fig. 19. Bacteria in the lumen of a caecal crypt. Some bacteria indent the plasma membrane (arrows)

Discussion

The food sources of primates can be classified into three major groups, depending on their structure and biochemical composition, and resulting digestibility (CHIVERS and HLADIK 1980). These are fruits, leaves and animal matter. "Fruits" include unripe (e.g. flowers) and ripe (fleshy) parts, seeds and tubers, i.e., mostly the reproductive parts of plants, which are foods containing short-chain sugars that are hydrolyzed rapidly for absorption and immediate use. "Leaves" include young and mature leaves, grasses, stems and also barks and gums, i.e., the vegetative parts of plants, which are foods usually containing protein and long-chain sugars that require fermentation in an enlarged stomach or large intestine. "Animal matter" includes invertebrates and small vertebrates, which provide sources of protein and fat that are easily digested and, therefore, require a relatively short and simple gut (CHIVERS and HLADIK 1980).

C. m. erythrarchus has the following percentage volumetric dietary composition for 713 plant food items scored in the Cape Vidal dune forest: fruits 69.2%; leaves 23.6%; animal matter 4.8%; other 1.6% (LAWES 1986, unpubl. data). Thus, the Samango is a typical frugivore (CHIVERS and HLADIK 1980), subsisting predominantly on fruits and supplementing the diet with varying amounts of leaves and insects. Fruits are easily digested and absorbed, while leaves require a fermentation process if a maximal energy return from the foliar component of the diet is to be achieved (MILTON 1981). From a knowledge of the diet and the gastric anatomy of the stomach and caecum of *C. m. erythrarchus*, it is possible to speculate on the digestive and foraging strategy used by the animal and whether a fermentation process is likely in the gut.

Stomach

The stomach of *C. m. erythrarchus* is a simple glandular unilocular sac, typical of the subfamily Cercopithecinae (HILL 1958; LANGER 1985). In the stomach three main glandular areas of the mucosa, the cardiac, fundic and pyloric regions, are identified. The gastric

secretions of proteolytic enzymes, hydrochloric acid and mucus are associated with these three areas of the stomach (LANGER 1985).

The well-developed gastric muscle layers and numerous rugae of the adult may facilitate mechanical digestion (the mixing, grinding and soaking of digesta) and provide a greater surface area for secretion, respectively, possibly as a result of the greater nutritioinal demand of the adult monkey. The primarily frugivorous diet of the Samango, however, does not require much mechanical breakdown in the stomach. The last premolars of frugivores tend to become molariform to provide additional crushing and grinding surfaces (MAIER 1984), while the cusps and edges of the molars of the Samango are bunodont (low and blunt). Thus, foods can be masticated to such a degree as to allow the maximum surface area for digestion, and the function of the rugae in the adult may simply be to provide a greater surface area for the production and release of gastric secretions.

Bacteria were present in both adult and juvenile Samango stomachs. It is highly unlikely, however, that the presence of small numbers of bacteria in the unilocular (ancestral, unspecialized; CARLETON 1973) stomach is indicative of a fermentation process (MADDOCK 1981). Where microbial fermentation occurs in the stomach, a voluminous fermentation vat is differentiated, holding food for fermentation and slowing the transit of digesta through the stomach (LANGER 1984b). The wholly glandular unilocular stomach of *C. m. erythrarchus* is obviously not suited to this function, since there is no physical or physiological separation of digestive processes in the fore and hindstomach. This is supported by the variable but high pH, as a decline to a low pH would destroy any bacteria present.

The stomach of *C. m. erythrarchus*, therefore, likely functions in the initial digestion of the high energy, easily digestible soluble carbohydrate and protein component of the diet. It is highly unlikely that any bacterial cellulolytic fermentation occurs, and although some initial gastric digestion of the foliar component may occur in the stomach, fermentative breakdown of leaves must surely occur elsewhere in the gut.

Caecum

No multicellular animal is known to synthesise cellulase and in consequence the animal is deprived not only of the nutrient value of the cellulose itself, but also of the digestible cell contents bounded by the cellulose wall (JANIS 1976). Therefore a great advantage can be gained by an animal that can include fibrous components in its diet by entering into a symbiotic association with cellulase-producing bacteria, but it must provide a fermentation chamber within the digestive tract where these bacteria can digest the cellulose (JANIS 1976).

The importance of the caecum and colon in fermentation processes has been determined for many herbivorous mammals (CURRIER et al. 1960; JOHNSON and MCBEE 1967; YANG et al. 1968; MCKENZIE 1978; SNIPES 1978, 1979; CLEMENS and PHILLIPS 1980; CLEMENS and MALOY 1981; VAN HOVEN et al. 1981; SNIPES 1981, 1982a, b, 1984a, b). It is possible that the caecum of *C. m. erythrarchus* functions as a fermentation chamber for the breakdown of the protein and fibre-rich leaf component of the diet, and evidence for this speculation is delivered in the investigation.

The major products of the fermentation of carbohydrates are usually the volatile fatty acids (VFAs), acetic, propionic and butyric (and methane). Fermentative activity is usually measured by determining VFA concentration in a portion of the alimentary tract (PARRA 1978). The presence of these organic acids along the digestive tract of non-ruminant herbivores has been demonstrated in vivo repeatedly (RERAT 1978); their concentrations are very large and reach a maximum at the level of the caecum and colon. Studies on four species of African Cercopithecinae have confirmed this distribution of VFAs along the digestive tract (CLEMENS and PHILLIPS 1980; CLEMENS and MALOY 1981). The concen-

tration of organic acids in the stomach is low, with lactic acid representing over half the total amount. Their concentration remains low in the small intestine but increases abruptly in the caecum and proximal half of the colon, where the passage of digesta is probably slowed down greatly by the taeniae and haustra (CLEMENS and PHILLIPS 1980; CLEMENS and MALOY 1981). The high concentrations of VFAs are strong evidence for an extensive microbial fermentation in the caecum and colon of these four primate species.

Microbial fermentation within the digestive tract of primates is a relatively new concept (CLEMENS and PHILLIPS 1980). With the exception of the Colobinae with their complex foreguts (BAUCHOP and MARTUCCI 1968; OHWAKI et al. 1974), it was believed until recently that primates were generally incapable of fermenting and digesting complex carbohydrates. However, the concentration of organic acids produced in the caecum and colon of the baboon, Sykes monkey, Vervet monkey and bushbaby (CLEMENS and PHILLIPS 1980; CLEMENS and MALOY 1981) are comparable to those observed in the foregut of ruminants and the hindguts of dogs, pigs and ponies (SWENSON 1982).

Considerable numbers of bacteria (representing a large biomass) are present in the caecum of *C. m. erythrarchus* and the close association of many bacteria with the epithelium is striking. In the Koala (*Phascolarctos cinereus*) the close association of bacteria with the epithelium aids absorption by epithelial cells of the products of microbial fermentation (MCKENZIE 1978). In the Samango, an actual penetration of bacteria into the epithelium is not evident, as was characteristic in the Koala. Rather, the adherence of the bacteria to the epithelium is in the form of an intermicrovillar location of the bacteria. Together with the large numbers of bacteria found among food particles, the presence of the adhering bacteria suggests that the caecum and microflora function symbiotically as a fermentation vat.

In *C. m. erythrarchus* the pH values along sections of the gastrointestinal tract are very similar to those recorded for two congeneric primate species, *C. mitis* and *C. pygerythrus* (CLEMENS and PHILLIPS 1980; CLEMENS and MALOY 1981). High concentrations of VFAs were present in the caeca of these two species, leading to a lowering of the pH. Due to the similar pH values along the GIT of all three species and the fact that high concentrations of VFA's have been observed in *C. mitis* and *C. pygerythrus*, it seems likely that the low pH in the caecum of *C. m. erythrarchus* is a result of the presence of high concentrations of VFAs. These acids are formed as breakdown products of microbial fermentation; this evidence, together with the observed large biomass of bacteria, also suggests that the caecum functions as a fermentation chamber. These aspects of physiology are to be investigated in *C. m. erythrarchus*.

The close proximity of ileocaecal and caecocolical orifices has been observed in previous studies (SNIPES 1981, 1982a, b). This is interpreted as providing the possibility of a rapid transport of intestinal contents directly from ileum to colon, thereby by-passing the greater portion of the caecum (SNIPES 1982b). This probably occurs with protein-rich, fibre-poor foodstuffs. Protein-poor and fibre-rich foodstuffs, however, require long-term fermentation activity for the necessary breakdown of cellulose, which would occur in the body of the caecum under optimal fermentation conditions (SNIPES 1982b). The presence of extensive musculature in the ileocaecal junction of *C. m. erythrarchus*, which appears to act as a valve/sphincter, could aid this directional flow, thereby enabling optimal fermentation conditions to persist in the caecum.

The possible significance of caecal and colonic taeniae and resulting huastra has been discussed by GABELLA (1982 op. cit. SNIPES 1982b, 1984a). He implies that the condensation of the longitudinal muscle into narrow bands (taeniae) may represent a specialization allowing mixing and movement of contents, as would be favourable for a "fermentation-vat" function of the caecum. Haustra are interpreted as advantageous for the fermentation process, acting as areas for slowing the rate of passage of digesta and thus allowing the process of fermentation to occur in a more suitable environment (LANGER 1979; CLEMENS

and PHILLIPS 1980; LANGER 1984a). The possession of well developed taeniae and haustra along the caecum and colon again strongly suggests active fermentation in these regions.

The striking structural differences between adult and juvenile caeca may be attributable to the fermentation process. The adult possesses a relatively small caecum with numerous folds and a large, haustrated colon, while the juvenile has a large caecum and a relatively small colon. In the adult, although caecal fermentation almost certainly occurs, colonic fermentation may be more important to the monkey. In the juvenile the colon has not developed to adult size and the caecum is proportionately larger and possibly more important in the fermentation process. JOHNSON and McBEE (1967) state that caecal fermentation in the porcupine (*Erethizon dorsatum epixanthrum*) appears to be of increasing importance in larger, older animals, and that this could be offset by younger animals having a proportionately larger caecum (JOHNSON and McBEE 1967).

Four major facts exemplify the importance of hindgut fermentation as an energy source in *C. m. erythrarchus*:

1. The presence of taeniae and haustra in the caecum and colon.
2. The resulting slow rate of passage of digesta (GABELLA 1981 op. cit LANGER 1979; SNIPES 1984a).
3. The presence of numerous bacteria interspersed within the microvilli.
4. The high VFA concentrations in congeneric species with similar anatomies and pH values.

However, the extent of the fermentation process in the caecum and colon of *C. m. erythrarchus* is not known at present and is the subject of further investigation.

Conclusion

It is possible to interpret the morphology of the stomach and caecum of *C. m. erythrarchus* in terms of the dietary requirements of the animal. The Samango eats primarily fruit (LAWES 1986 unpub. data), which is generally rich in nonstructural carbohydrates but low in protein. The simple, glandular stomach provides copious secretions of acids and enzymes necessary for the breakdown of the high quality and easily digestible fruit component, with consequent high utilisation of the nonstructural, soluble carbohydrates. However, the Samango supplements its primarily frugivorous diet with a considerable amount of foliar material (23.6 % of dietary composition). Leaves are high in protein and structural carbohydrates, and to maximize energy returns from leaves requires slow passage rates of food for microbial fermentation to occur. The convoluted caecum and capacious colon of the Samango both possess taeniae and haustra, which slow down the passage rate of food and suggest that an active fermentation process occurs. This ensures maximal energy returns from the foliar component of the diet and from undigested fruit pectins. The caecal and colonic fermentation would be particularly important in mid-winter when food quality and abundance is low, and Samango's experience a "crunch" period with a relatively nutrient-poor diet.

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